



Below and above-ground carbon distribution along a rainfall gradient. A case of the Zambezi teak forests, Zambia

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ABSTRACT

Understanding carbon (C) stocks or biomass in forests is important to examine how forests mitigate climate change. To estimate biomass in stems, branches and roots takes intensive fieldwork to uproot, cut and weigh the mass of each component. Different models or equations are also required. Our research focussed on the dry tropical Zambezi teak forests and we studied their structure at three sites following a rainfall gradient in Zambia. We sampled 3558 trees at 42 plots covering a combined area of 15ha. Using data from destructive tree samples, we developed mixed-species biomass models to estimate above ground biomass for small (< 5 cm diameter at breast height (DBH, 1.3 m above-ground)) and large (≥ 5 cm DBH) trees involving 90 and 104 trees respectively, that belonged to 12 species. A below-ground biomass model was developed from seven trees of three species (16–44 cm DBH) whose complete root systems were excavated. Three stump models were also derived from these uprooted trees. Finally, we determined the C fractions from 194 trees that belonged to 12 species. The analysis revealed that DBH was the only predictor that significantly correlated to both above-ground and below-ground biomass. We found a mean root-to-shoot ratio of 0.38:0.62. The C fraction in leaves ranged from 39% to 42%, while it varied between 41% and 46% in wood. The C fraction was highest at the Kabompo site that received the highest rainfall, and lowest at the intermediate Namwala site. The C stocks varied between 15 and 36 ton C ha⁻¹ and these stocks were highest at the wetter Kabompo site and lowest at the drier Sesheke site. Our results indicate that the projected future rainfall decrease for southern Africa, will likely reduce the C storage potential of the Zambezi teak forests, thereby adversely affecting their mitigating role in climate change.

1. Introduction

The Zambezi teak forests form part of the dry tropical forests of southern Africa and cover about 265000 km² in north-western Zimbabwe, north-east Botswana, south-west Zambia, north-east Namibia, and south-east Angola. These forests are found at elevations of between 900 m and 1100 m on the gently undulating plateau overlain by deep Kalahari sands (Timberlake et al., 2010). About 2.6% (of 265000 km²) of these forests are found in central, north-western, southern, and western provinces of Zambia (Chidumayo, 1997) across a south-north climatic gradient with annual rainfall ranging from

700 mm in the south to 1100 mm in the north. The Zambezi teak forests cover 9% of the total forest extent of 453000 km² in Zambia (Matakala et al., 2015). *Baikiaea plurijuga* Harms is the dominant tree species in these teak forests (Mbughi, 1986; Mulolwa, 1986; Pearce, 1986; Ngoma et al., 2017) and the forests' ground layer is covered by herbs and grasses that normally facilitate the spread of fire during the dry season (Mulolwa, 1986).

Because of the species diversity, the benefits from the Zambezi teak forests are also many, ranging from economic, social, and ecological. Economically, the forests are important because of valuable commercial timber coming from the *Baikiaea Plurijuga* that supply local, national

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and international markets (Mubita, 1986; Musokotwane and Kufakwandi, 1986; Peele, 1984; Pearce, 1986). In Zambia, logging in the Zambezi teak forests is dated back to 1911 when the first sawmill began operating in Livingstone. Between 1964 and 1970, 450,000 m³ of *Baikiaea plurijuga* and other species were removed annually from the forests for both commercial and domestic usage (Musokotwane and Kufakwandi, 1986). By 1986, there were five sawmills utilizing the Zambezi teak forests mainly producing railway sleepers, mining sleepers, parquet battens, and sawn timber from the *Baikiaea plurijuga* Harm (Pearce, 1986).

The Zambezi teak forests provide social benefits to the local people through the provision of food, medicine, and firewood (Kwashirai, 2007). People are also provided with employment through wood based industries (Pearce, 1986). Ecologically, the forests conserve biological diversity (FAO, 2007) and provide natural habitat for fauna and flora (Mubita, 1986; Kwashirai, 2007). Catchment areas are also protected (FAO, 2007). Scientific, educational and aesthetic value are some of the additional benefits of the Zambezi teak forests (Pearce, 1986).

In addition to these benefits is the role the forests play in mitigating climate change. Plants take up significant amount of CO₂, thereby acting as carbon sinks (Sarmiento and Gruber, 2002). However, despite the forests being so important, deforestation and climate change are some of the threats of the Zambezi teak forests. If these forests disappeared, the whole genetic pool would be lost as these forests are only found in southern Africa. It is therefore important that carbon stocks of these forests are established. Literature (Brown and Lugo, 1984; Chidumayo, 1990; Brown et al., 1991; Malimbwi et al., 1994; Brown SaG, 1996; Chave et al., 2003; Baccini et al., 2008; Henry et al., 2009;

Hertel et al., 2009; Kamelarczyk, 2009; Shirima et al., 2011; Gautam and Pietsch, 2012; Ullah and Al-Amin, 2012) shows that tropical forests hold different amounts of biomass and carbon stocks. Unfortunately, these biomass and C stocks have not been accurately quantified. Quantification of biomass requires the use of allometric models, which are currently lacking for these forests despite similar models being available for other forest types (e.g. Henry et al. (2011)). Thus, developing ecosystem-specific biomass models for the Zambezi teak forests is crucial to reduce uncertainties and achieve more accurate results in C accounting in dry tropical forests. The objectives of our study were (1) to develop allometric equations for estimating component biomass of the Zambezi teak forests; (2) to evaluate the C fraction in component biomass of these teak forests; and (3) to assess C stocks along a rainfall gradient in these teak forests.

2. State of the Zambezi teak forests

The Zambezi teak forests have experienced various forms of forest degradation and deforestation. Apart from timber production, deforestation and forest degradation have also been caused by agricultural expansion, wood fuel collection, bush fires and infrastructure development underpinned by demographic and economic changes (Theilade et al., 2001; Matakala et al., 2015; Musgrave, 2016). The Zambezi teak forests have lost half of their area since 1975 due to logging and agricultural activities among others (Musgrave, 2016), and this trend has increased since 1984 (Fig. 1). This indicates that, with the recent increase in Zambian population from about 13 million to 15 million (The Government of the Republic of Zambia, 2016), coupled with poor

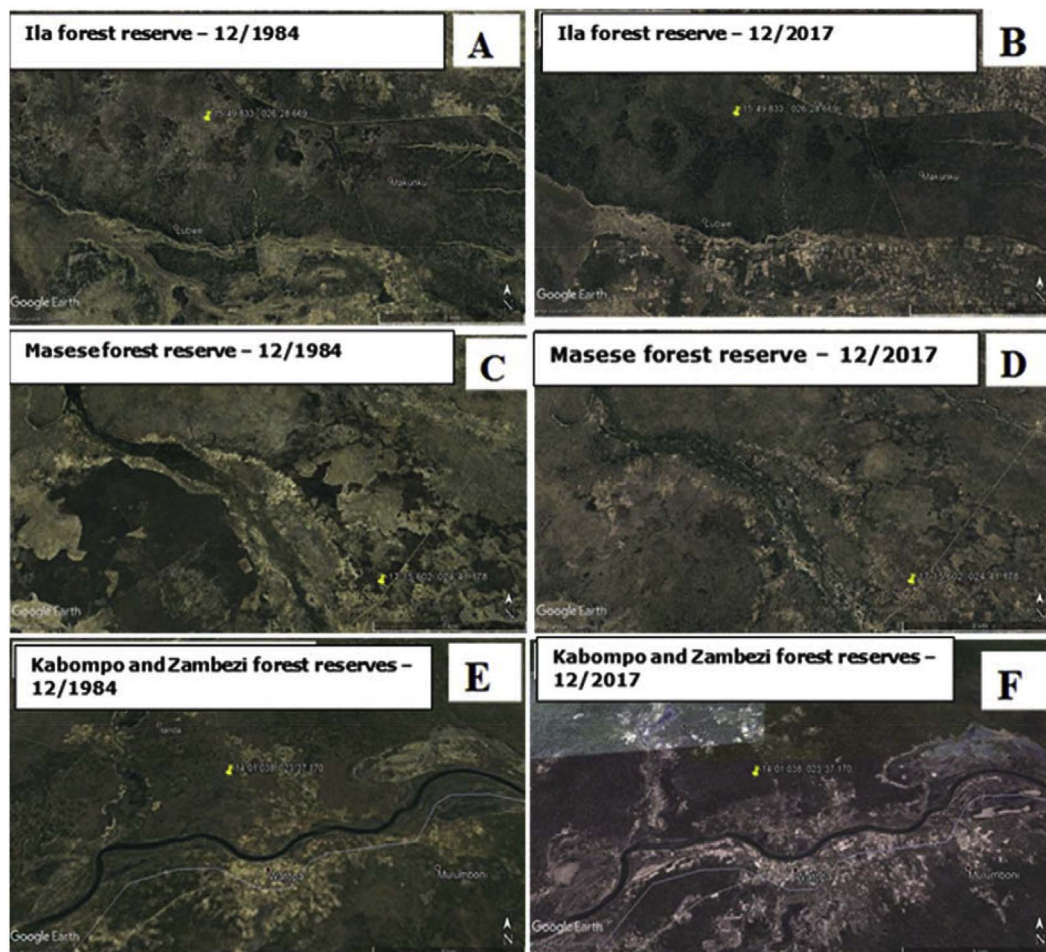


Fig. 1. Status of the Zambezi teak forests in some of the reserves. Ila forest reserve in December 1984 (A) and in December 2017 (B); the Masese forest reserve in December 1984 (C) and in December 2017 (D); Kabompo and Zambezi forest reserves in December 1984 (E) and in December 2017 (F) ((Masese Forest Reserve, 2017)

implementation of forestry monitoring programs, the extent of these forests will probably reduce even further.

3. Materials and methods

3.1. Study sites

Zambia is divided into three ecological zones defined by the amount of annual rainfall (Fig. 2). Zone I receives less than 700 mm and zone II receives between 800 mm and 1000 mm. The wetter Zone III receives more than 1000 mm (The Government of the Republic of Zambia and UNDP, 2009). Our research was carried out at sites in the Kabompo (14°00.551S, 023°35.106E), Namwala (15°50.732S, 026°28.927E), and Sesheke (17°21.278S, 24°22.560E) areas (Study sites). In Kabompo, the study was carried out in Kabompo and Zambezi Forest Reserves, which are part of Zone II. The Sesheke study site is part of the Masese Forest Reserve, which is located in Zone I. The Namwala study site is part of the Ila Forest Reserve on the transition between Zones I and II (Figs. 2 and 3).

We used rainfall figures from local meteorological stations that were within a 200 km radius, but in the same ecological zones as the respective forest reserves where our vegetation assessments were conducted. All rainfall figures for the respective local meteorological stations were provided by the head meteorological office in Lusaka. We used rainfall values from Kabompo and the Zambezi meteorological stations for Kabompo site, while rainfall data for the Sesheke site came from the Sesheke and Livingstone meteorological stations. Namwala site was supplied with rainfall data from the Choma meteorological station. We averaged rainfall figures from various meteorological stations to allow us to fill data gaps from individual site records. In addition to their geographical locations, their accessibility through existing roads was another criterion we used to choose these study sites.

3.2. Plot size and number of plots

Optimal plot size was determined by assessing the maximum variation in stem density as a function of plot area. We implemented the plot size that gave maximum variation in stem density. A 3600 m² (60 m by 60 m) square plot size was adopted (Barker, 2001) (Fig. 4A). The total number of plots required was taken from the variability in stem densities

as a function of the number of plots. The optimal number of plots were taken as the maximum variation in stem density as a function of the number of plots (Fig. 4B). This is the point at which the relationship between the number of plots and the variation in stem density flattened (Fig. 4B). Thus, a total of fifteen plots (i.e. 5 plots per site) sufficed to capture the maximum variability in all sites. However, to secure a broader understanding of the forests, an additional nine plots were surveyed in each study site. Both the optimal plot size and the required number of plots were established by applying Google Earth Pro along with ArcGIS and by counting individual trees in the satellite images.

3.3. Forest assessment

A total of 42 plots were sampled for the complete forest assessment in all the sites. This covered an area of just over 15ha in which the DBH and total heights of all trees were measured. The protocol used in this research was based on the field manual prepared for the Integrated Land Use Assessment (ILUA) project of the Zambian Forestry Department (Branthomme et al., 2006). Fig. 5 represents the sampling design and Table 1 provides a more detailed sampling description. In each study site, the main plots were established to measure large diameter trees (≥ 5 cm DBH), 20 m by 20 m sub-plots to assess smaller diameter trees (< 5 cm DBH), 5 m by 5 m sub-plots to assess dead wood of less than 10 cm in diameter on the forest floor and 1 m by 1 m sub-plots for the sampling of tree regeneration (plants of less than 1 m height). We based the 60 m by 60 m plot size on our statistical analysis (Fig. 4; See Section 3.2) and all our sample plots were square (See Fig. 5). We classified small trees as trees smaller than 5 cm in DBH and taller than 1.3 cm in height, and regeneration as woody plants of less than 1 m height. We measured both live and dead trees including stumps. Trees were identified using local names in the respective study sites. The survey crew at each site included one elderly local person who was familiar with these local trees and helped to identify species. The local names were later linked to their botanical names using Storrs and Storrs (1979) and if no botanical name was found, these species were only specified by their local names.

3.4. Below-ground biomass and stump models

We sampled trees from the Masese Forest Reserve in Sesheke to

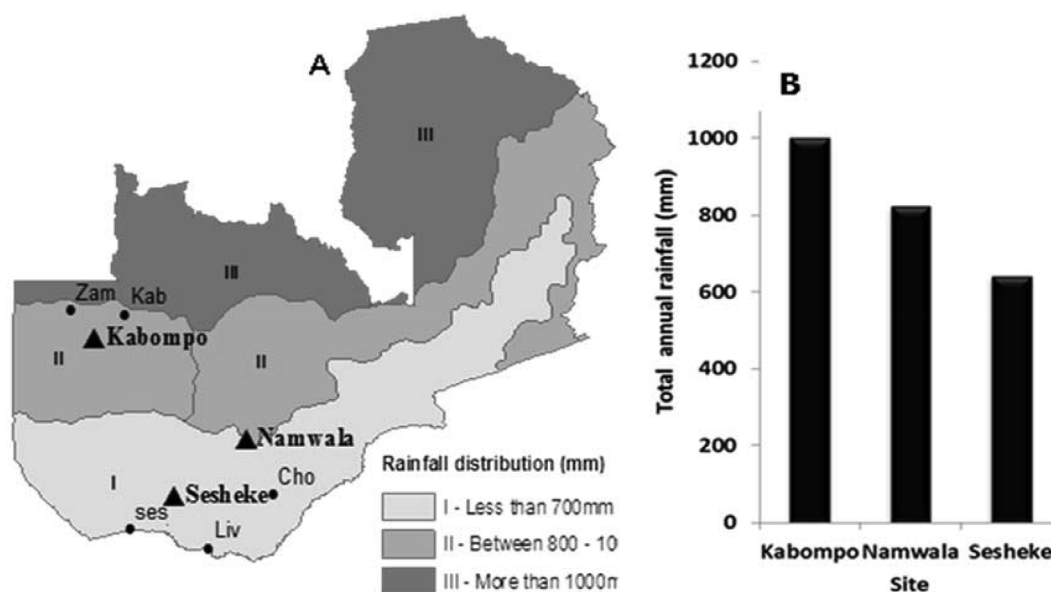


Fig. 2. (A) Ecological zones, distribution of study sites and meteorological stations. (B) Total annual rainfall received at Kabompo, Namwala and Sesheke sites. The total annual rainfall figures cover the period 1973–1989 (Kabompo), 1970–2011 (Namwala) and 1958–2011 (Sesheke) based on available data. The black triangles show study sites, while black dots show locations of meteorological stations. 'Zam' is Zambezi meteorological station and 'Kab' stands for Kabompo.

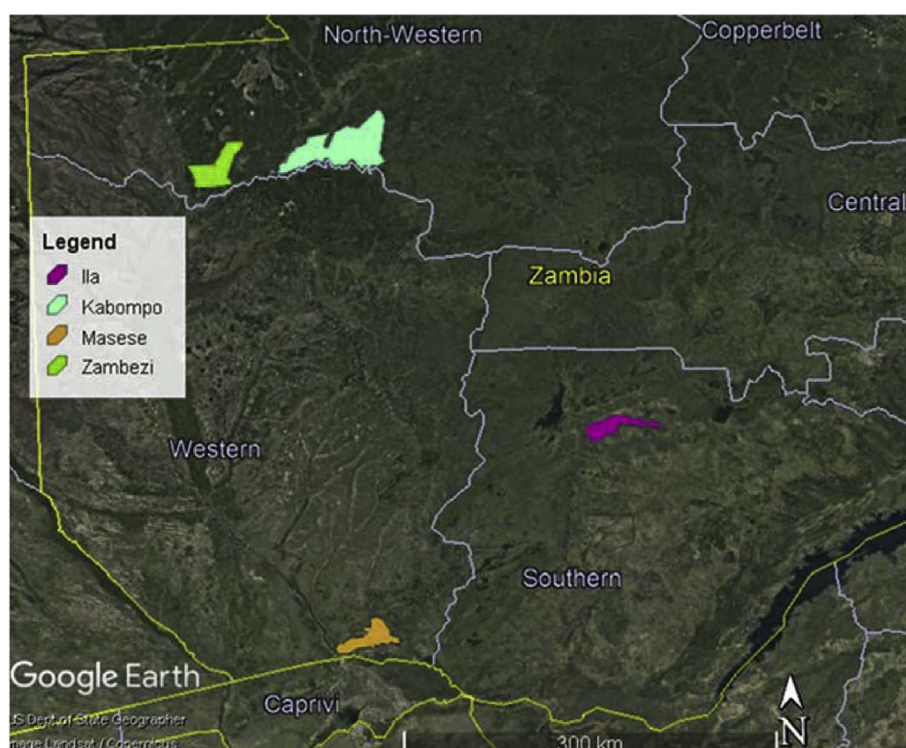


Fig. 3. Surveyed reserves of the Zambezi teak forests. (Masese Forest Reserve et al. (2017))

develop below-ground biomass and stump models. This reserve is located near a local community from which we drew labour to help in uprooting of trees. In total, seven trees of the species *Baikiaea plurijuga*, *Ficus sycomorus*, and *Lonchocarpus nelsii* with diameter size ranging from 15.7 cm to 44.0 cm were uprooted. Total tree height, DBH, crown heights, and crown diameters were measured before felling each tree (See Table 3 in Ngoma et al. (2018)). After felling a tree and measuring the above-ground biomass, roots were excavated by first exposing all the main roots that connect directly to the taproot. From this taproot, all roots were followed until they tapered to ≤ 5 mm in diameter. Roots were cut into smaller parts by a chainsaw and the soil was carefully removed by brushing. The roots were then weighed immediately to avoid water loss. Root mid-diameter and length were also measured (c.f. Fig. 1 in Ngoma et al. (2018) for the whole sampling process). A pre-weighed root disc was taken to the laboratory for dry weight determination. From the excavated trees, their stumps (measured at 30 cm

above ground level), were cut and weighed separately to get stump fresh weight. All stumps had the same height of 30 cm cut above ground level.

3.5. Above-ground biomass model

Trees and their respective species were selected after executing a DBH-based forest survey and calculating Cottam and Curtis (1956) Importance Value Indices (IVI). The IVI indicates the distribution of tree species in the reserves. The indices take into account not just the diversity or number of trees available in an area, but also the size of trees. Tree species with the highest IVI values were selected to regress the above-ground biomass models. The first three species with the highest IVI (in each category of large and smaller diameter trees) were selected at each site to collect their above-ground biomass (See Tables 4 and 5 in Ngoma et al. (2018)). Ten trees per category and species were targeted.

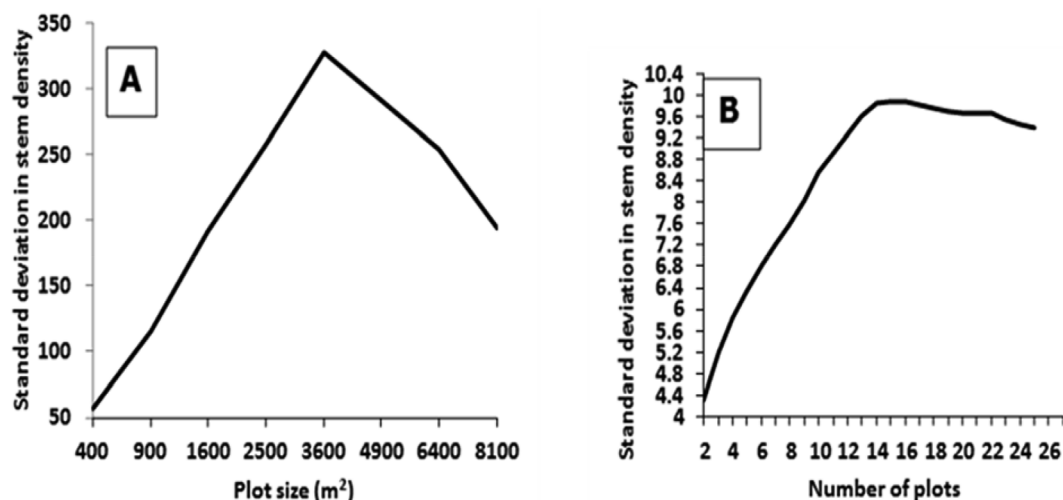


Fig. 4. (A) Plot size (B) Number of plots.

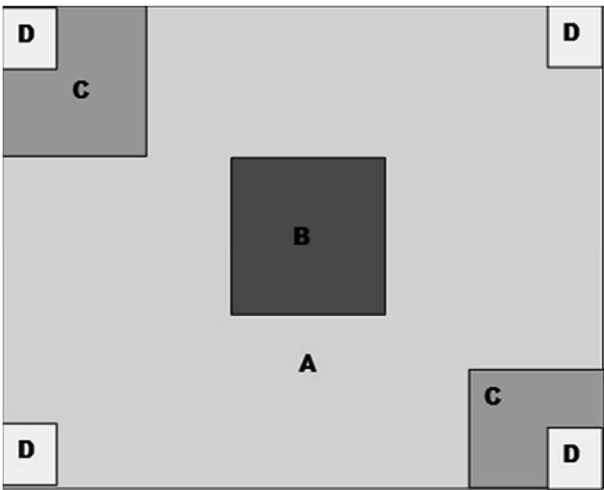


Fig. 5. Schematic representation of the sampling design. Main plots of 60 m by 60 m size (A) were established to measure large trees (≥ 5 cm DBH), 20 m by 20 m sub-plot (B) to assess small trees (1–4.9 DBH), 5 m by 5 m sub-plot (C) to assess dead wood of less than 10 cm mid-diameter lying on the ground and 1 m by 1 m sub-plots (D) to assess re-generation. All sub-plots were established systematically to avoid sampling bias. The data recorded at each plot and sub-plot are described in Table 1.

However, when felling a targeted tree, this tree could hit and fell a nearby tree. Both, the targeted and the injured trees were then weighed and include in our analysis. Three injured Namwala trees and four Sesheke trees were included in our above-ground samples. We also included the seven excavated tree samples from the Sesheke site.

To have a balanced tree size distribution in our regression analysis, trees of each species were grouped in five DBH classes for large trees (i.e. 5–10 cm, 11–20 cm, 21–30 cm, 31–40 cm and > 40 cm in DBH) and four classes for small trees (1.1–2.0 cm, 2.1–3.0 cm, 3.1–4.0 cm and 4.1–4.9 cm in DBH). Trees were distributed almost equally per diameter class per species. A total of 104 large trees (See Table 2 in Ngoma et al. (2018)) and 90 small trees (See Table 1 in Ngoma et al. (2018)) were cut and weighed to develop the above-ground biomass models. All samples were immediately weighed in the field to avoid the effect of moisture loss (c.f. Fig. 2 in Ngoma et al. (2018) for the whole sampling process). One pre-weighed stem (or trunk) disc from each felled tree was taken to the laboratory to determine its dry weight. We took trunk discs of smaller trees (< 5 cm DBH) and larger trees of up to 20 cm DBH at 30 cm above ground level. As for larger trees of more than 20 cm DBH, we sampled discs of 20 cm diameter from the branches of the respective trees. Diameters of discs sampled from the trunks differed with tree size. All discs were 3 cm–5 cm thick. We avoided getting very large discs because ovens in the laboratory were too small to accommodate these large discs.

3.6. Carbon content of stem, branches, roots, and leaves

We collected stem, branches, roots, and leaf samples from all trees that were harvested (See Tables 1–3 in Ngoma et al. (2018)) to determine their C fractions. One root disc (in the case of the Sesheke site) and one stem (or trunk) disc were taken from each felled tree (Details of wood discs were as described in Section 3.5). Root discs were taken from the taproot of each uprooted tree. Samples were taken from different locations in different tree components (e.g. some wood samples were taken from the trunks while other samples were taken from the branches of the sampled trees) which could affect comparability. To reduce this bias, we made composite samples from trunks and branches at the respective sites. Leaf samples were taken from the branches of each felled tree. Following the number of felled trees and species (See Tables 1–3 in Ngoma et al. (2018)), 194 stem discs and 7 root discs were collected from all sites. An A4-size envelope was filled with leaves

Table 1
Description of the sampling design (See also Fig. 5).

Plot	Plot size	Samples measured	Parameters measured in the field	Comments
A	60 m by 60 m	Standing live trees (≥ 5 cm DBH)	Total tree height, bole height, DBH, crown height and crown diameter.	Crown diameter was measured at the widest and thinnest parts of the crown (Schreuder et al., 1993). Tree heights, bole heights and DBH were measured following Branthomme et al. (2006). Trees were measured in the same way as standing live trees. We measured stump diameter at the top of the stump for all stumps that had heights of up to 30 cm above ground level. For stumps with heights of more than 30 cm above ground level, but less than 1.3 m above ground level, we measured their diameters at 30 cm above ground level. For stumps that were longer than 1.3 m above ground level, their diameters were measured at 1.3 m (DBH). Fallen trees were measured following Branthomme et al. (2006). Hollow wood was noted and length and diameters of the holes were measured (Harmon, 1996; Brown et al., 2004). From each lying wood, a sample was taken and immediately weighed to determine its 'fresh' weight. The pre-weighed sub-sample was taken to the laboratory for dry weight determination.
		Standing dead trees (≥ 5 cm DBH)	Total tree height and DBH	
		Stumps	Stump height and diameter	
B	20 m by 20 m	Dead wood lying on the ground (≥ 10 cm mid-diameter)	For whole lying tree, we measured total height and DBH. For lying pieces of wood, diameters were measured at base, mid and the top. Total length was also measured.	Smaller trees were measured the same way as the larger trees (Branthomme et al., 2006). Samples were harvested and immediately weighed. The pre-weighed sub-samples were taken to the laboratory for dry weight determination. We harvested the plants of less than 1 m height from the ground level and green weight weighed. Pre-weighed sub-samples were taken to the laboratory for dry weight determination.
		Live and standing smaller trees (< 5 cm DBH)	Total tree height and DBH	
		Dead and standing small trees (< 5 cm in DBH)	Total tree height and DBH	
C	5 m by 5 m	Dead wood lying on the ground (< 10 cm mid-diameter including twigs)	Wood 'fresh' weight	
D	1 m by 1 m	Regeneration	Fresh weight.	

Table 2

Number of species and trees inventoried per site.

Site	Total number of species			Total number of trees surveyed per site			Tree density (Number of trees per hectare)			Tree basal area (m ² ha ⁻¹)
	Large trees	Small trees	Large plus small	Large trees	Small trees	Large plus small	Large trees	Small trees	Large plus small	Large trees
Kabompo	33	19	37	1287	100	1387	255	179	248	10.01
Namwala	28	30	43	958	548	1506	190	979	269	7.36
Sesheke	18	13	25	457	208	665	91	371	119	4.55
All sites	70^a	55^a	80^a	2702	856	3558	179	510	235	7.31

^a The total number of species in all sites is NOT the summation of species in the respective sites as some species were common among sites. Large trees had DBH ≥ 5 cm and small trees fall between 1.1 and 4.9 cm DBH. Note that small and large trees were respectively surveyed in 400 m² and 3600 m² plot sizes.

Table 3

Model parameters and performance criteria.

Diameter class (cm)	Tree component estimated	Model number	Model type	Model	AIC	RSE _{train}	LOOCV	MAPE (%)	Parameter a	Parameter b	r ²
5.0–70.0	Above-ground tree biomass	1	log-log	Log(AGB) = a + b • Log(DBH)	96.5986	0.3777	0.1450	93.6731	–2.3295	2.4028	0.94
		2	Power	AGB_L = a • (DBH)^b	1360.8272	164.7390	34821.5580	–19.8839	0.1232	2.3586	N/A
1.1–4.9	Above-ground tree biomass	3	log-log	Log(AGB) = a + b • Log(DBH)	108.1889	0.4893	0.2433	200.8378	–1.9348	2.1572	0.81
		4	Power	AGB_s = a • (DBH)^b	224.3459	1.0726	1.2673	–22.6336	0.1148	2.4586	N/A
15.7–44.0	Below-ground tree biomass	5	log-log	Log(BGB) = a + b • Log(DBH)	8.2886	0.3371	0.1186	91.1292	–2.9239	2.2778	0.94
		6	Power	BGB = a • (DBH)^b	75.2345	40.2302	2223.2173	–20.0011	0.1259	2.0488	N/A
15.7–44.0	Above-ground stump biomass	7	log-log	Log(AGS) = a + b • Log(SD)	8.2052	0.3561	0.1315	84.4883	–6.4064	2.7790	0.91
		8	Power	AGS = a • (SD)^b	45.6624	8.0768	90.6690	1.1543	0.0004	3.1897	N/A
15.7–44.0	Above-ground biomass of harvested trees estimated from stump diameter.	9	log-log	Log(AGB _h) = a + b • Log(SD)	8.5166	0.3655	0.1677	97.2692	–3.4557	2.6185	0.90
		10	Power	AGB_h = a • (SD)^b	80.4303	146.3965	98981.4074	5.7290	0.0045	3.1440	N/A
15.7–44.0	DBH from stump diameter	11	log-log	Log(DBH) = a + b • Log(SD)	–2.5897	0.1449	0.0223	87.0386	–0.3421	1.0415	0.90
		12	Power	DBH = a • (SD)^b	38.2717	4.3627	21.3339	–1.9357	0.8371	0.9974	N/A

Symbols AGBL = Above-ground tree biomass of a large tree (kg), AGBs = Above ground biomass of a small tree (kg), AGBh = Above ground biomass of a harvested tree (small and large) (kg), DBH = Diameter at breast height (cm), BGB = Below-ground biomass (kg), AGS = Above-ground stump biomass (kg), SD = Stump diameter (measured at 30 cm above ground level, cm), RSE_{train} = Residual standard Error on training data (units follow the units of dependent variable), LOOCV = Leave-Out-One-Cross-Validation (units follow the units of dependent variable), MAPE = Mean Absolute Percentage Error (%), AIC = Akaike Information Criteria. All recommended models are in bold.

Formulas AIC = $-2 \cdot \ln(\text{likelihood}) + k \cdot \text{npar}$ (Sakamoto et al., 1986; Aho et al., 2014), $\text{RSE} = \sqrt{\left(\frac{\text{RSS}}{n-2}\right)}$, $\text{LOOCV}(n) = \frac{1}{n} \sum_{i=1}^n (\text{MSE}_i)$, $\text{MSE} = \frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2$ (Gareth et al., 2013), $\text{MAPE}(\%) = \frac{100}{n} \left(\frac{\text{Observation} - \text{Prediction}}{\text{Observation}} \right)$ (Sileshi, 2014)
npar = number of parameters in the fitted model, k = 2, n = number of observations, MSE = mean Square Error, RSS = Residual Sum of Squares.

from each felled tree and 194 leaf samples (envelopes) were taken. A total of 395 samples from twelve tree species were collected to determine their C fractions in various tree components (i.e. stem, branches, roots, and leaves).

3.7. Laboratory analysis

Fresh wood and root samples were weighed in the field to avoid moisture loss. We then determined the volume of these pre-weighed samples in the laboratory before oven drying them for 24 h at 105 °C to get their dry weight. Due to the irregular nature of the samples, volume was determined by water displacement in the ‘as received condition’ since the samples were partially dry by the time they reached the laboratory from the study sites. Sample volume was taken as the amount of water displaced following mode IV in the ASTM (2007). We determined density (g cm⁻³) from the dry mass (g) and sample volume (cm³). To quicken the laboratory process, we analysed half of the samples at the Copperbelt University and another half at the Division of the Forestry Research of the Zambian Forestry Department.

We ground stem, branches, roots, and leaves into fine powder before analysing them for their C fraction. C fractions were determined by

Fisons EA1108 CHN-0 elemental analyser at the Ecosystem Laboratory of Wageningen University and Research. The analyser was monitored for accuracy of reading every ten samples with the Atropina standard (70.56% C, 4.84% N).

Table 4

Mean C fraction as a percentage of total molecular weight of all elements in tree biomass per site per species. Figures in brackets are the standard deviations.

Species	Kabompo (%)	Namwala(%)	Sesheke (%)
<i>Baikiaea plurijuga</i>	44.4 (3.9)	42.8 (4.3)	42.5 (5.1)
<i>Baphia massaiensis</i>	43.4(3.4)	35.4 (4.5)	43.3 (2.3)
<i>Combretum celastroides</i>	–	41.5 (7.8)	–
<i>Combretum hereroense</i>	–	–	42.6 (4.3)
<i>Diplorhynchus candylocarpon</i>	43.6 (1.2)	38.5 (5.5)	–
<i>Entandrophragma caudatum</i>	–	–	39.8 (4.7)
<i>Ficus sycamoros</i>	–	–	39.7 (3.0)
<i>Friesodielsia obovata</i>	–	41.2 (3.1)	40.1 (3.5)
<i>Lonchocarpus nelsii</i>	–	–	39.6 (3.6)
<i>Pterocarpus angolensis</i>	–	40.8 (4.2)	–
<i>Pteleopsis anisoptera</i>	44.5 (4.4)	–	–
<i>Pterocarpus antunesii</i>	–	–	41.6 (2.7)
Average	44.0 (3.2)	40.5(4.9)	41.3(4.0)

Table 5

Carbon fraction as a percentage of total molecular weight of all elements in various tree components of tropical trees for this and other studies.

Study	Stem or trunk wood (%)	Leaf (%)	Wood roots (%)	Laboratory method and equipment used
This study	34–53	31–51	34–40	Gas chromatography on a CHN-O Elemental analyser, EA1108 (Fisons instruments).
IPCC. (1996)	46–49	43–47		Various methods
Kraenzel et al. (2003)	47–51	46–48	45–49	Gas chromatography on a CHN Elemental analyser, EA1108 (Fisons instruments)
Arias et al. (2011)	47–50	41–50		Carlo Erba Analyser 1500
Negi (2003)	41–46	26–44		Ash content method and by regression equation derived between carbon and Calcium content (%).
Hughes et al. (2000)	45–49	43–47		Induction- furnace method using a Carlo-Erba NA Series 1500 CNS analyser (Fisons Instruments, Danvers, Massa- chusetts, USA)
Bert and Danjon (2006)	52–54		51–52	Dumas method with a Leco CN2000 analyser
Thomas and Martin (2012)	47–49			Literature review
Becker et al. (2012)	47–50			Elementary-analyser, Elementar Vario EL
Elias and Potvin (2003)	42–51			Automated elemental analyser (model EA 1108, Fisons Instruments, Milan, Italy).
Martin and Thomas (2011)	45–50			ECS 4010 CN analyser (Costech Analytical Technologies Inc., Valencia, CA, USA)
Chambers et al. (2001)	49			Fisons C/N auto-analyser
Rana et al. (2010)	47–48			CNS analyser (Vario L, Hanau, Germany).

3.8. Data analysis

The data were analysed in R environment (R Core Team, 2017). We used NLSTOOLS package (Baty et al., 2015) to fit non-linear regressions and we determined the Leave-One-Out Cross Validation (LOOCV) of these non-linear regressions using the MASS package (Venables and Ripley, 2002). Linear regressions were fitted using the STATS package (R Core Team, 2017) and the LOOCV of these linear regressions were determined using the BOOT package (Davison and Hinkley, 1997). We applied the models that we developed in this study (Table 3), to estimate biomass stock. To determine the volume of dead pieces of wood lying on the ground (> 10 cm mid-diameter), we used Newton's formula (Kershaw et al., 2016):

$$V = \frac{L}{6} (A_b + 4A_m + A_t)$$

where, V = Volume (m³), L = Length of log (m), A_b = Area at the base (m²), A_m = area at the middle (m²), and A_t = Area at the top (m²) of the wood lying on the ground.

This volume was used together with wood density of the sampled trees to determine the biomass of dead wood. Dry weight of small dead wood material (< 10 cm mid-diameter) lying on the ground and regeneration were estimated by direct weighing.

3.9. Model regression, selection, and evaluation

The most common model types developed for dry tropical forests range from exponential, power, linear, logarithmic, to polynomial models (Henry et al., 2011). These models are based on single species and multiple species using one variable or multiple variables. However, we tested the power model following the different allometry theory that predict universal scaling relationships between the dependent variable (Y) and independent variable (x) (Niklas, 1995; West et al., 1999; Sileshi, 2014). We also tested the log-log model (Niklas and Spatz, 2004; Sileshi, 2014).

- (i) Power model: $Y = a \cdot X^b$
- (ii) Log-log model: $\ln(Y) = a + b \cdot \ln(X)$

We first ran a multiple regression to determine the predictor (independent) variables that had significant influence on the response (or dependent) variable ($p < 0.05$). For the two categories of large and smaller trees, we further conducted a Shapiro-Wilk Normality Test ($p < 0.05$) to check whether the population (combined data of large and small trees) was normally distributed. Following the results of multiple regression and a Shapiro-Wilk Normality Test, we developed models using predictor variables that significantly influenced the

response variables.

We selected the best-fit models based on Mean Absolute Percentage Error (MAPE) (Sileshi, 2014). Models with lower values of MAPE were recommended. We reported values of Akaike Information Criteria (AIC) (Sakamoto et al., 1986; Symonds and Moussalli, 2011; Gareth et al., 2013; Sileshi, 2014) and Residual standard Error (RSE)¹ (Gareth et al., 2013) for information. The AIC estimates the relative information lost when a given model is used to represent the process that generated the data. Thus, for competing model candidates, the best model is the candidate model that minimises information loss. For models with more than one predictor variable, the AIC also imposes a penalty and acts as a guard against overfitting of parameters. We further carried out a LOOCV (Gareth et al., 2013) to provide more information on how the models would perform on independent data. Coefficient of determination (r^2) values were reported for linear models (Spiess and Neumeyer, 2010) only. The AIC, RSE, and LOOCV can also be used individually or in combination to measure the performance of the models by selecting the best fit models with the lowest values. However, we did not use these values as criteria for model selection in our study since the reported AIC, RSE, and LOOCV values could not be compared for power-law models in the arithmetic ($Y = a \cdot X^b$) and logarithmic ($\ln(Y) = a + b \cdot \ln(X)$) domains.

4. Results

4.1. Vegetation structure

A total of 3558 trees of diameter class 1.1–70.0 cm were inventoried. This enabled us determine vegetation and biomass structures at the Sesheke, Namwala, and Kabompo sites. Thus, tree density was highest at the Namwala (265 trees ha⁻¹) and the least number of trees were surveyed at the Sesheke site (119 trees ha⁻¹). Kabompo had 248 trees ha⁻¹. Of the 80 species recorded, Namwala had the highest diversity of 43 species (c.f. Table 2).

4.2. Allometric models

A multiple regression ran between the response variable (biomass) and predictive variables (i.e. DBH, total tree height, and wood density) showed that only DBH ($p < 0.0001$) had significant effects on tree biomass. Total tree height ($p = 0.618$) and wood density ($p = 0.711$) did not significantly relate to biomass. The Shapiro-Wilk Normality Test ($p < 0.05$) showed that the combined data of large and small trees

¹ $RSE = \sqrt{RSS/(n-2)}$, where RSE = Residual standard Error, RSS = Residual Sum of Squares, and n = sample size (Gareth et al., 2013).

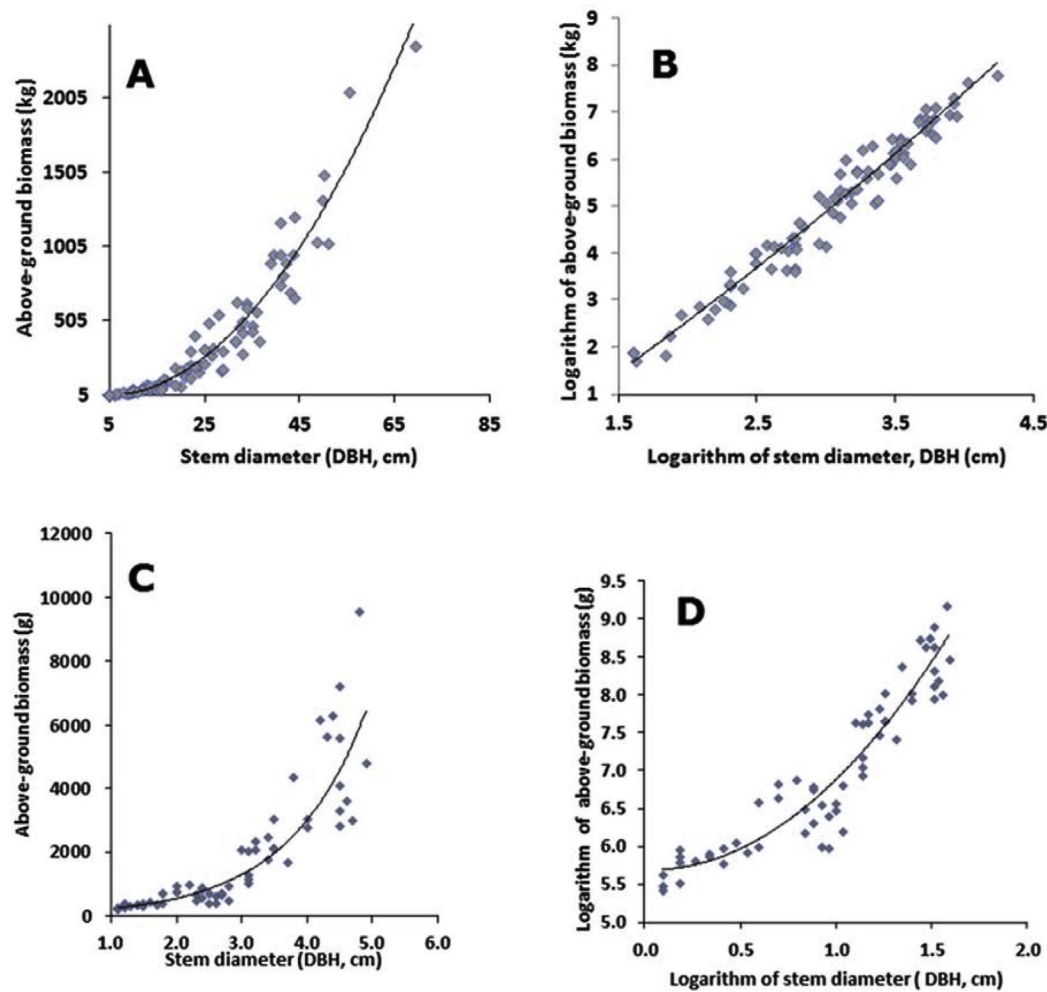


Fig. 6. Regression plots and lines of best fit on above-ground biomass models data sets of: (A) large trees before log transformation; (B) large trees after log transformation; (C) small trees before log transformation; and (D) small trees after log transformation.

were not normally distributed ($p < 0.0001$). DBH was thus the only robust independent variable in above-ground and below-ground biomass models and we developed separate models for large (≥ 5 cm DBH) and small (< 5 cm DBH) trees (see Fig. 6).

Using the criteria from Section 3.9, we recommended Models 2 and 4 (Table 3) to estimate above-ground biomass of large and small trees respectively. While Model 6 was recommended to estimate biomass in roots, we recommended Model 8 to estimate biomass in stumps and Model 10 to estimate above-ground biomass of trees that have been harvested from the forest (See Table 3). Model 12 fitted well in estimating DBH of trees that have been harvested already from the forests. We found an average root-to-shoot ratio of 0.38:0.62 (See Table 3 in Ngoma et al. (2018)).

4.3. Forest carbon assessment

4.3.1. Carbon fraction in wood, roots, and leaves

The twelve tree species assessed in the Zambezi teak forests had an average C fraction of 42% with the highest fraction recorded at the Kabompo site (Table 4). The C fraction was highest in *Pteleopsis anisoptera* (45%) while *Ficus sycomorus* recorded the lowest C fraction (40%) (Fig. 7 and Table 4) for the carbon distribution per species per site). Wood (i.e. Stem and branches) stored the most C compared to leaves and roots (Fig. 7). The ANOVA showed that wood C and leaf C strongly differed and this difference was significant at the Kabompo ($p = 0.006$) and Namwala ($p = 0.022$) sites, and insignificant at the Sesheke ($p = 0.644$) site. The C fraction in wood differed significantly

between Kabompo and Namwala ($p = 0.010$). We did not find any significant difference in C fractions of leaves among sites. Roots had an average C fraction of 36% with the highest fraction recorded in *Ficus sycomorus* (37%) (Fig. 7A).

4.3.2. Forest biomass and carbon stock

We estimated biomass using the better models selected in this study (See Table 3 and Section 4.2). Above-ground biomass was highest at the Kabompo site (56 t ha^{-1}) compared to Namwala (39 t ha^{-1}) and Sesheke (25 t ha^{-1}) sites. Of the 80 species surveyed, *Baikiaea plurijuga* recorded the highest above-ground biomass stock of 72 t ha^{-1} , while other species had varying amounts of biomass stocks. Lying deadwood was also highest at the Kabompo site (4 t ha^{-1}) compared to the Namwala (3 t ha^{-1}) and Sesheke sites (1 t ha^{-1}). However, deadwood did not significantly differ between the Kabompo and Namwala sites ($p = 0.692$). Stump biomass was highest at the Namwala (0.64 t ha^{-1}) compared to Kabompo (0.48 t ha^{-1}) and Sesheke (0.17 t ha^{-1}) sites. Below-ground biomass was 38% of above-ground biomass. However, below-ground biomass attached to stumps for the trees that were cut from the forests, was highest at the Namwala site. This showed similar patterns to above-ground biomass in stumps. A similar pattern was observed for biomass that was removed through different human activities (e.g. logging). About 7 t ha^{-1} of biomass was removed in Namwala while Kabompo lost 5 t ha^{-1} . Sesheke lost only 2 t ha^{-1} . We recorded 0.06 t ha^{-1} of biomass of regeneration at Kabompo, 0.34 t ha^{-1} at Namwala and 0.07 t ha^{-1} at Sesheke.

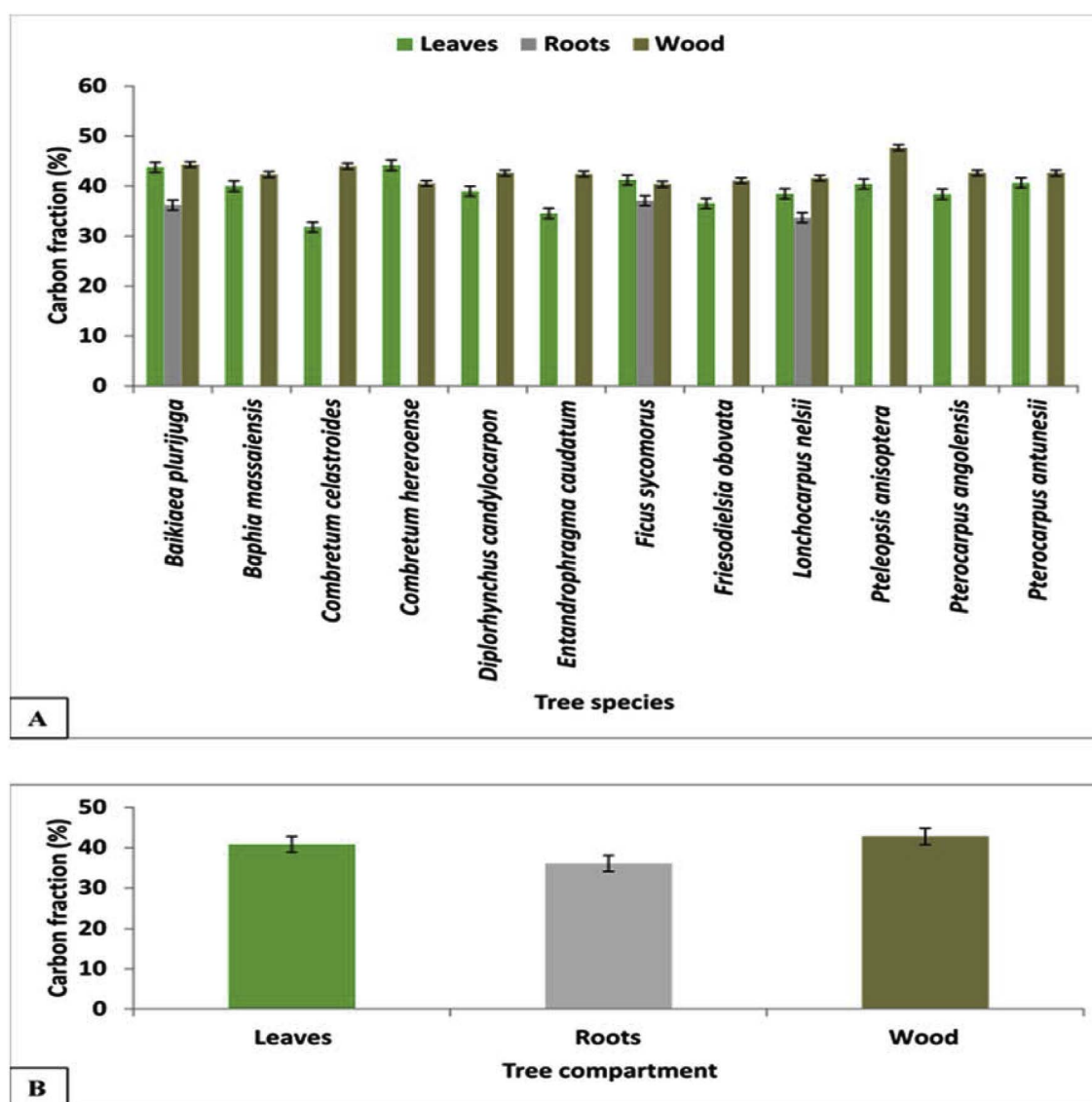


Fig. 7. Carbon fraction as a percentage of total molecular weight of all elements in wood (i.e. stem and branches), leaves and roots. (A) presents the Carbon fraction per species per compartment and (B) summarizes the carbon fraction per compartment.

Biomass stock (t ha^{-1}) was converted to C stock (t C ha^{-1}) by average site specific C factors of 43.98, 40.47 and 41.31% at the Kabompo, Namwala, and Sesheke sites respectively. Kabompo had 36 t C ha^{-1} compared to Namwala and the Sesheke sites, which had 25 t C ha^{-1} and 15 t C ha^{-1} respectively (Fig. 8). We found the highest C stock in *Baikiaea plurijuga* at all sites (c.f. Table 6 in Ngoma et al. (2018)).

5. Discussion

5.1. Allometric models

The power model in an arithmetic domain performed better than the log-log model for both large and small trees including stumps. However, the performance of these models could not easily be compared with similar models (Henry et al., 2011) due to the different indicators used to measure their performances. While we used MAPE (Sileshi, 2014), other researchers (Henry et al., 2011) used other indicators such as the Mean Square Error (Chave et al., 2005) and Root Mean Square Error (Jibrin and Abdulkadir, 2015). Although no standard performance criteria have been created to compare different

models, some of our models' results were significantly better. For example, Model 2 performed best for above-ground biomass of large trees. The high influence of DBH on tree biomass that we found, is consistent with many other studies on tropical trees (Brown et al., 1989; Chidumayo, 1990; Deans et al., 1996; Brown, 1997; Chamshama et al., 2004; Chave et al., 2005; Basuki et al., 2009; Lima and Suwa, 2012).

Most studies (Henry et al., 2011) have reported coefficient of determination (r^2) values for non-linear models. This indicator can be used to measure the performance of linear models, but cannot be used in the same capacity for nonlinear models since the total sum of squares (TSS) is not equal to the summation of the regression sum-of squares (REGSS) and the residual sum-of-squares (RSS) (Spiess and Neumeyer, 2010). We therefore did not report r^2 - values for the non-linear power models in this study. Moreover, the r^2 - value increases when polynomial terms are added (Sileshi, 2014), and also when sample size is reduced. This makes r^2 a weak indicator to use as a criteria in model selection. Although we used 12 species only to develop the models out of the 80 species we recorded during our vegetation assessments, we included the most common and dominant species in an effort to reduce bias. We developed below-ground biomass models using trees from the driest Sesheke site due to limited resources. Excavation of trees is

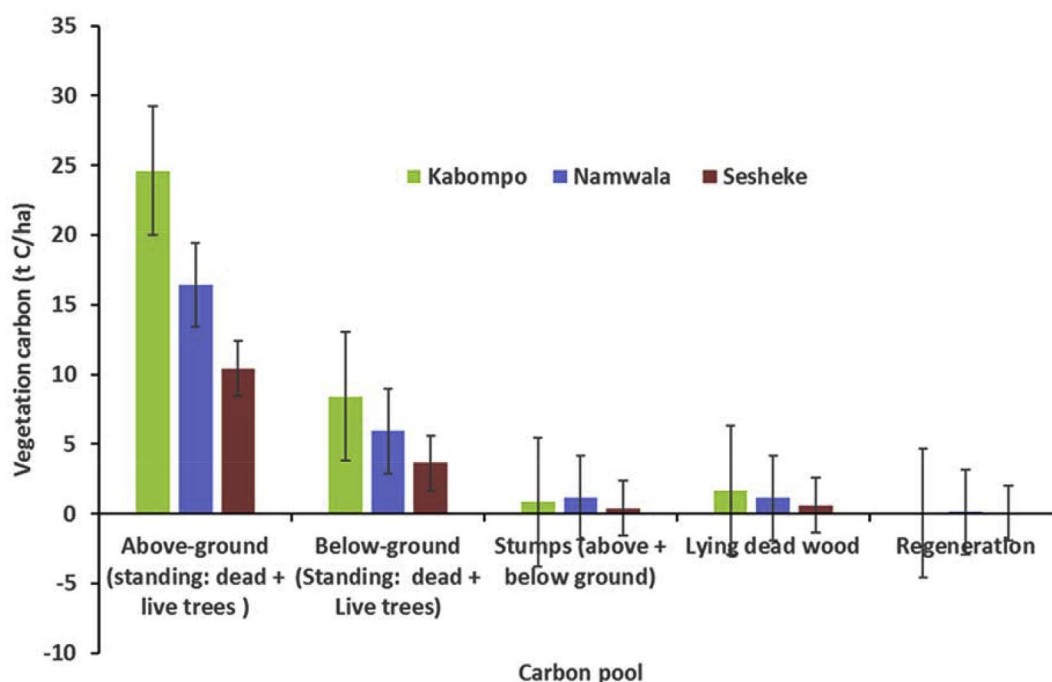


Fig. 8. C Stock distribution within and among sites.

Table 6

Above-ground biomass stock in tropical dry forests. Dry forests receive less than 1000 mm rainfall annually (IPCC, 1996).

Study	Above-ground biomass stock (t ha ⁻¹)	DBH range (cm)	Place of study
This study	25–56	≥ 1 cm	Zambia
Kamelarczyk (2009)	32–51	≥ 7 cm	Zambia
Chidumayo (1993)	49–91	≥ 1 cm	Zambia
Chidumayo (1990)	78–107	> 5 cm	Zambia
Chamshama et al. (2004)	23–44	≥ 5 cm	Tanzania
Shirima et al. (2011)	19–27	≥ 10 cm	Tanzania
Brown (1997)	20–175	≥ 10 cm	Africa
Brown (1997)	16–70	≥ 10 cm	Asia

extremely expensive and labour intensive. Moreover, roots of the studied trees grow very deep and wide (Höglberg, 1984; Childs, 1988). For example, the lateral roots of the uprooted trees spread 28 m away from the taproot base. The taproots tapered to 5 mm diameter at about 6 m deep.

Both above and below-ground samples were generated through destructive sampling (See Ngoma et al. (2018)). These sampling processes introduce errors through the loss of wood and root material when cutting. However, measures were taken to reduce this error by using a chain saw with a narrow kerf size and correcting for width of the cut.

The root-to-shoot ratio of 0.38:0.62 was in line with other dry tropical tree studies. For example, while Malimbwi et al. (1994) found a root-to-shoot ratio of 0.25:0.75, Castellanos et al. (1991) reported 0.42:0.58, Mugasha et al. (2013) 0.40:0.60, and Kraenzel et al. (2003) 0.16:0.84. Ryan et al. (2011) reported a root-to-shoot ratio of 0.42:0.58 for dry tropical forests. Differences in actual root-to-shoot ratios could be due to differences in the species studied, the sample size, the size of the trees sampled, sampling methods, and the minimum diameter of the roots that were included in the ratio calculations. For example, Deans et al. (1996) included roots of 10 mm as a minimum diameter while Castellanos et al. (1991) included roots of 5 mm diameter. This study included roots of minimally 5 mm diameter. While we completely excavated all roots of the sampled trees, other researchers (e.g. Mugasha

et al. (2013)) relied on sampling of the roots. The root-to-shoot ratio of our study decreased with increasing DBH ($r = -0.26$). This means that, even though the ratio can be applied on smaller trees, some bias in the results of the small trees will occur.

The developed stump models require that stump diameter is measured at a height of 30 cm above-ground level or below. For stumps with sprouts, only biomass of stumps is estimated by these models. This indicates that stump biomass is under-estimated by these models. Stump models also facilitate biomass estimates of trees that have been removed through timber extraction. This is often not done because appropriate models are unavailable. We carefully measured a stump height of 30 cm and this increased the reliability of our models.

5.2. Carbon fraction in wood, leaves and roots

The C fraction is a function of different factors including species, tree age, climate, soil conditions, and chemical composition (Elias and Potvin, 2003; Bert and Danjon, 2006; Koss et al., 2007). High lignin content in wood, for example, increases the C fraction (Bert and Danjon, 2006). We found higher C fraction in wood than in leaves. This was also reported by other studies (Table 5). For example, Kraenzel et al. (2003) found a C fraction of 50% in wood and 47% in leaves. The C fraction was highest in *Pteleopsis anisoptera* and lowest in *Lonchocarpus nelsii*. Following the rainfall gradient, the C fraction increased with increasing rainfall (Fig. 9). This was most evident in *Baikiaea plurijuga* and *Baphia massaiensis*, which were both found in all the three sites. The C fraction in *Baikiaea plurijuga* was 4% higher at the wetter Kabompo site than at the drier Sesheke site.

The C fraction at the Kabompo and Sesheke sites shows a clear difference in C storage potential of trees with changes in rainfall (Fig. 9). Our results show the lowest C fraction at the Namwala site. The Namwala's Ila forest reserve stretches both in the dry and wetter zones. Here, trees are likely affected more by the local drier conditions than the wetter conditions. Comparing the reported annual rainfall and C fraction figures, trees at the Namwala site do not seem to store as much C. The Choma meteorological station probably reported rainfall values that do not represent the actual amount of rainfall received by the Ila forest reserve due to the 200 km distance between the meteorological station and the forest reserve.

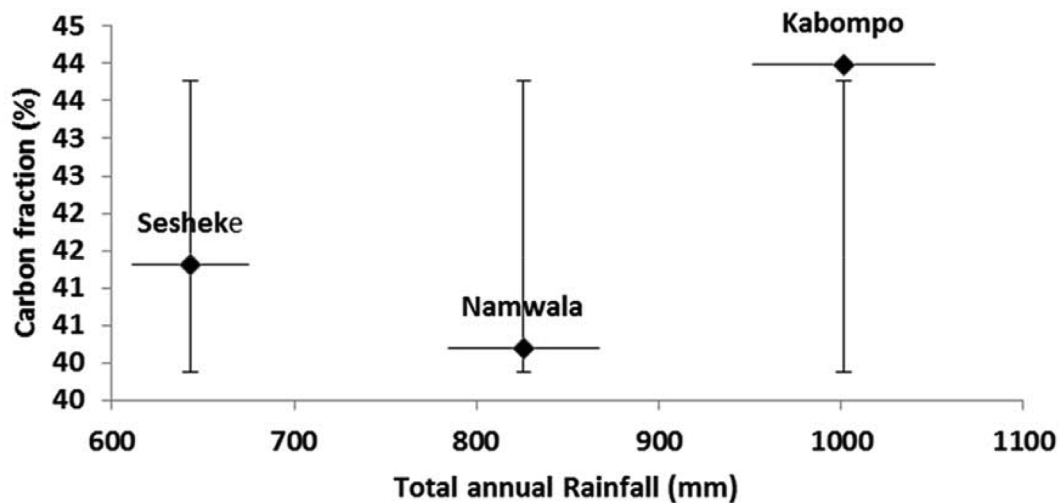


Fig. 9. Inter-site carbon fraction as a percentage total molecular weight of elements in tree biomass in relation to rainfall.

The reported C fractions were within the values reported by other studies on tropical trees (Table 5). The variability in actual numbers (See Table 5) are probably due to differences in species, sample size, sampling strategy (e.g. heartwood, sapwood, small trees and large trees), variability in environmental conditions, and laboratory methodologies (Table 5).

5.3. Biomass and carbon stock

Above-ground biomass was highest at Kabompo, despite having lost 5 t ha^{-1} of wood from logging activities. Increased biomass at Kabompo is due to high tree density. This increased tree density probably resulted from higher regeneration after the logging activities and then further stimulated by the higher rainfall.

A total of 7 t ha^{-1} was lost at Namwala from logging activities, but its biomass stock was still higher than at Sesheke that lost only 2 t ha^{-1} from logging. The higher rainfall at Namwala as compared to Sesheke, increased tree basal area and tree density. The lower biomass at Sesheke correlated well with low rainfall, tree density and low tree basal area.

The above-ground biomass stock values reported in this study are generally within the range reported by other studies on tropical dry forests (Table 6). Conversion of total biomass stock (t ha^{-1}) to total C stock (t C ha^{-1}) led to the highest C stock at the Kabompo site compared to the Namwala and Sesheke sites. The total C stock per hectare is a function of total biomass per hectare and the average C fraction. Both biomass stock and average C fraction were highest at the Kabompo site. This explained in the highest C stock. Though the C fraction was lowest at the Namwala site, its C stock was higher than at the Sesheke site. This high Namwala C stock was explained by its high biomass stock, which is likely a consequence of increased tree density more than high basal area. In general, *Baikiaea plurijuga* had the highest C stock. This most abundant tree species represents a quarter of all surveyed trees of the 80 species. Comparably, carbon stock values reported in this study are within the range of values reported for Zambian forests (Kamelarczyk, 2009).

So far, we have done a one-time forest assessment which could define a baseline. To obtain trends in C storage potential of these forests, such assessments should be carried out repeatedly (e.g. after every ten years). The Zambian Forestry Department should stimulate such developing monitoring program and should work with local communities to better manage these forests and their reserves.

6. Conclusions

The power-law models in arithmetic domain performed better than the log-log models for large and small trees including stumps. DBH was

the most important factor in developing both below and above-ground biomass models, thereby reducing the need to measure other parameters, such as total tree heights, in forest inventories. Stump biomass models helped to capture biomass in stumps and thereby improved the total forest biomass estimates. Generally, mature trees in the Zambezi teak forests have more C stock above-ground than below-ground. We recorded the highest C stock at the Kabompo site followed by the Namwala and Sesheke sites respectively. However, more C stock was lost due to logging at the Namwala site than at the Kabompo and Sesheke sites. The C fraction was highest at the Kabompo site, closely followed by the Sesheke site and lowest at the Namwala site. *Pteleopsis anisoptera* had the highest C fraction whilst *Lonchocarpus nelsii* had the lowest C fraction. This indicates differences in C storage potential of trees of dry tropical forests. Of the 80 species surveyed, the dominant *Baikiaea plurijuga* had the highest C stock. However, both C fraction and C stock increased with increasing rainfall. This study therefore suggests that a rainfall decrease for southern Africa, as projected by Niang et al. (2014) for future climate change could negatively affect carbon stock of the Zambezi teak forests through its effects on forest productivity. These negative effect, coupled with forest degradation and deforestation (Musgrave, 2016), also as observed in our sites, will likely reduce the C stocks. The reduced carbon stock will negatively affect the C storage potential of the studied Zambezi teak forests resulting in decreased mitigating role in climate change.

Statement of authorship

Justine Ngoma, Rik Leemans, Eddy Moors, Bart Kruijt and Royd Vinya conceived the idea and designed the study, Emmanuel N. Chidumayo guided on field data collection, Justine Ngoma conducted field and laboratory work, Justine Ngoma and Emmanuel N. Chidumayo analysed the data, Justine Ngoma wrote the manuscript, James H. Speer together with all other authors provided editorial comments, interpreted and discussed the results. All authors have approved the final article and declare that no conflict of interest exists.

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laboratory technicians at the Zambian Division of Forestry Research in Kitwe to allow us using their facilities and assisting in the analyses. We further appreciate the guidance of Mr. Felix Chileshe at Copperbelt University and Mr. Jan Van Walsen at Wageningen University during the final analyses. We finally thank Mr. Andrew Kamwi and Mr. Gershom Ndumba for providing practical information on the study sites and how to get there.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2018.02.003>.

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